

The Adult Behavior of the Japanese Cabbage White (Lepidoptera, Pieridae) in the Field

I. Behavior Repertoire Observed

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Synopsis Based on the continuous trailing of particular adults of *Pieris rapae crucivora* BOISDUVAL in an open field, 35 behavior patterns were described. A table for the combination of movable body parts was applied to 17 patterns.

Introduction

The ethogram is a catalog of all behavior patterns exhibited by a particular species. Based on field observations, ethograms are available for many mammals and birds (e.g. ALTMANN, 1965; RUSSEL, 1970; DUBOST, 1971, 1975; MASATOMI & KITAGAWA, 1975; FEIST & McCULLOUGH, 1976; RASA, 1977). Few attempts have been undertaken to make such catalogs for insects except for social aculeates (e.g. WALLIS, 1962; OHTANI, 1974, 1977; GADAGKAR & JOSHI, 1983; KASUYA, 1983a, b). Evidently, this bias depends on interest in the behavioral complexity of these insects as well as on their fixed nests sites which can be easily observed. Many investigators may have been discouraged from trailing non-residential volant insects to make ethograms.

The Japanese cabbage white, *Pieris rapae crucivora* BOISDUVAL, is one of the most common butterflies in the Holarctic, but most close descriptions on their behavior patterns have not been carried out, except for mating behavior (OBARA & HIDAKA, 1964; OBARA, 1964; SUZUKI *et al.*, 1977) in field cages.

My colleague (Dr. M. YAMAMOTO) and I attempted to understand the entire adult life of the butterfly as a stream of consecutive behavior patterns under field conditions. The present paper is one of the relevant studies based on our respective observations (cf. YAMAMOTO & OHTANI, 1979; OHTANI & YAMAMOTO, 1980; YAMAMOTO 1981a, b, 1982).

The method adopted in this study is 'longitudinal', i.e. the continuous trailing of a particular individual, as already employed for the intranidal behavior of the European honeybee (LINDAUER, 1952; OHTANI, 1974, 1977). Although a consecutive observation inevitably stops when the individual is lost, the execution of a 'longitudinal' method in the field may be favorable for comprehension of the entire life mode or the ecological outline.

What are indispensable for closer analyses, however, are 'cross-sectional' observations (i.e. detailed ones of a particular behavior for many individuals) in the field

and precise observations and experiments with individuals in field cages and laboratory. In this sense, the present study gives an 'open catalog', to which new categories can be added *ad libitum* (ALTMANN, 1965).

Materials and Methods

Descriptions and characterization of various behavior patterns were made by observing both marked and unmarked adults. For continuous observation of particular individuals pupae of different generations were collected from the campus of Hokkaido University (Fig. 1) from April to August in 1976.



Fig. 1. Study field on the campus of Hokkaido University. Photo showing the relatively poor vegetation in early July.

Newly emerged adults (8 males and 12 females) and fresh adults from the field (3 males and 8 females) were individually marked with quick drying ink (red points on upperside of fore wings, red numbers on underside of hind wings, Fig. 2). Most of

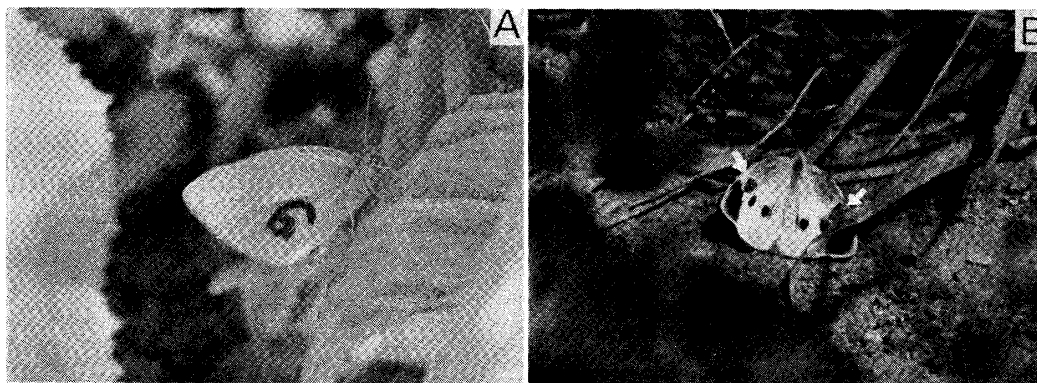


Fig. 2. Marked individuals. A: Numeral mark on the underside of hind wings of a male resting on a leaf. B: Dot marks on the upperside of fore wings (white arrows) of a female resting on soil.

the adults were followed immediately after they were released or after a female mated with an unmarked field male. While paying attention to cause minimal disturbance, 2 observers followed each marked individual all day long. Observation continued day after day until the marked butterfly died or until it was lost. A stream of behavior patterns of a particular individual was recorded on the original sheets (cf. OHTANI, 1984) scaled at 5-s intervals.

Air temperature was taken every hour and changes of other weather conditions were also recorded. Micro-climatic conditions around each concerned butterfly were not recorded.

Results and Discussion

The general description of 17 behavior patterns is expressed by the combinations of positions and movements of main body parts: proboscis, antennae, head, legs, wings and abdomen (Fig. 3, Table 1). Mating behavior is omitted in Table 1 because the interactions which occurred between males and females are not completely expressed in the table. *Excretion* is also omitted because of insufficient data (only one case).

Various behavior patterns are divided into 2 categories, *unit behaviors* which can be treated separately, and *temporally integrated behaviors* which appear as a definite sequence of several patterns. Unit behaviors are subdivided into *solitary behaviors*

Table 1. A list of behavior patterns characterized by positions (p) and movements (m) of main body parts. Explanations for figures are given in Fig. 3. Arrows indicate transitional state. Gothic figures denote the most frequent state.

Behavior patterns (Abbreviations)	Proboscis		Antennae		Head		Legs		Wings		Abdomen	
	p	m	p	m	p	m	p	m	p	m	p	m
<i>Resting (Re)</i>	1		2		1		1	(3) ^a	0~3		1	
<i>Hanging (Ha)</i>	1		2		1		2	(3) ^a	0		1	
<i>Sleeping (Sl)</i>	1		1		1		2		0		1	
<i>Self-cleaning (Sc)</i>	1		2,3		1,2	1	1		0~3		1	
<i>Head rolling (Hr)</i>	1		2,3		1	1			0~3		1	
<i>Walking (Wa)</i>	1		2,3		1		2		0~3		1	
<i>Nectar intake (Ni)</i>	2	1	2		2	1,2	2		0~3		1	
<i>Water intake (Wi)</i>	2	1	2		2	1	2		0~3		1	
<i>Feeding (FE)</i>												
<i>Flying (FL)</i>	1		?		1?	?	3			4	1,2	
<i>Fluttering (Ft)</i>	1		2,3		1		1			3	1	
<i>Taking-off (To)</i>	1		2,3		1		1→3		0~3→4		1	
<i>Wing folding (Wd)</i>	1		2,3		1		1,2		1~3→2		1	
<i>Leaning (Le)</i>	1		2,3		1		1,2	3	0~2		1	
<i>Abdomen erecting (Ae)</i>	1		2,3		1		1		2~4←1		2←1	
<i>Egg laying (El)</i>												
<i>Drumming (dr)</i>	1		1,2		1		1,2	4	0~3	3	1	
<i>Pressing abdominal tip (pr)</i>	1		1,2		1		1,2	2	0~3		2	
<i>Oviposition (ov)</i>	1		1,2		1		1,2		0~3		3	

^a *Le* appears during *Re* and *Ha*.

and *interindividual behaviors*. Solitary behaviors appear without intervention of other individuals, while interindividual behaviors are each composed of mutual responses of 2 or more individuals and their abbreviations include information on actor and actee, e.g. *cAb/d* (active behavior *Ab* by actor *c* to actee *d*), *c/Abd* (passive response *Ab* by actee *d* given to active behavior by actor *c*), and *c-Ab-d* (reciprocal behavior between individual *c* and individual *d*). 'Maintenance behaviors' and 'social behaviors' are not used, as functions of some behavior patterns are not always clear.

For all behavior patterns, abbreviations are used in both singular and plural cases. Unit behaviors are given by the combination of capital and lower-case letters (e.g. *Re*, *Wa*). The combination of 2 capital letters (e.g. *IN*, *FL*) denotes a convenient group of some similar unit behaviors. Temporally integrated behaviors are postulated as governed by a drive¹⁾, and several component patterns appear in temporally linked succession. These components do not appear in isolation, so their abbreviations are given by combinations of lower-case letters (e.g. *kc*, *pa*).

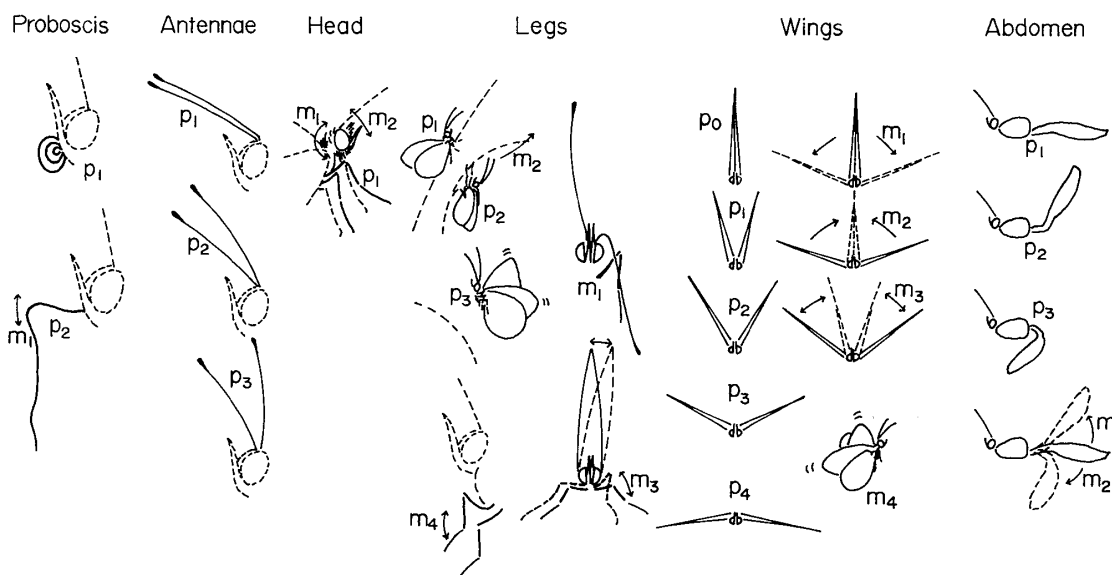


Fig. 3. Positional grades and kinds of movements of main body parts. Proboscis: (*m*₁) exploring by protruding proboscis. Head: (*m*₁) rolling laterally; (*m*₂) up-and-down movement. Legs: (*p*₁) sitting; (*p*₂) hanging; (*p*₃) no contact with substrate at flying; (*m*₁) wiping body part; (*m*₂) walking; (*m*₃) leaning; (*m*₄) fore-leg tapping. The positions and movements of wings and abdomen have no names. All are adopted in Table 1.

The situation at which a behavior pattern appears or disappears is inevitably observed. It is abbreviated to ST, which is useful to know the relationship with other patterns.

I. Solitary behaviors

1. Inactivity (*IN*): Including 3 patterns; *resting*, *hanging* and *sleeping*.

¹⁾ The application of this term should be precisely defined (cf. HINDE 1966: 194–202), but in this paper, it is used informally to refer to internal conditions such as hunger, thirst, or sexual urge.

1) *Resting (Re)*: The awakened state (cf. Fig. 3, antenna, p_2) in sitting on plants and other substrata (Fig. 2).

Dr. YAMAMOTO and I observed 'sun-bathing' (wings opened, head turned away from the sun) at low air temperatures, and 'sun-avoiding' (wings closed, head turned toward the sun) at high temperatures, but we could not find clear differences between them and *Re*. Therefore, we did not attempt to distinguish them from *Re*, though FUKUDA *et al.* (1972), OHSAKI (1983) and OBARA (1983) referred to 'sun-bathing'.

ST: Mostly after *flying*, sometimes intervened by *walking*, *head rolling*, *wing folding*, *leaning*, *fluttering* and *abdomen erecting*. Mostly followed by *taking-off* and *fluttering*. In females *Re* often alternates with *egg laying*.

2) *Hanging (Ha)*: The awakened state in hanging from plants after copulation, under showery or too hot weather conditions.

ST: After *flying*, esp. *roost-searching flight*. The behavior patterns inserted during *resting (Re)* also appear here. Followed by *fluttering*, *Re* or *sleeping*.

3) *Sleeping (Sl)*: The non-awakened state (cf. Fig. 3, antenna, p_1) at night, showing little or no response to artificial interference such as moving a net, touching the grass near the butterfly, blowing on butterfly's body, etc.

ST: After *roost-searching flight*. Followed by *resting (Re)* or *walking* in the next morning.

2. *Self-cleaning (Sc)*: Head cleaning with both fore legs was the only type observed, occurring in 17 out of 19 cases in females studied. With alternate and swift movements of forelegs.

JANDER (1966) often observed eye cleaning by coincidental movements of both fore legs in Hesperiidæ and Papilionidæ, but in *Pieris napi* alternate movements of fore legs occurred. According to him, pierid butterflies do not clean their antennae since they lack a tibial spur on their legs.

ST: During *resting (Re)*. Often followed by *flying* a few min later.

3. *Head rolling (Hr)*: Rolling head alone. No movement of fore legs, otherwise good resemblance to the above head cleaning (*Sc*).

ST: Followed by *flying* (24.8%) and *resting (Re)* (69.3%). In the latter cases, often followed by *flying* about 5 s later (males: 2/23; females: 13/47).

4. *Walking (Wa)*: Locomotion by using all legs.

ST: Mostly (9/13) during *resting (Re)* or *hanging (Ha)*, mediating change from *Ha* or *sleeping (Sl)* to *Re*, i.e. butterflies walked from hanging or sleeping sites to 'sun-bathing' places in the morning. In 3 cases inserted between *flying*.

5. *Feeding (FE)*: Sucking liquid with proboscis. Divided into nectar and water intake.

1) *Nectar intake (Ni)*: Sucking nectar from flowers.

ST: Inserted during *resting (Re)* and *flying*.

2) *Water intake (Wi)*: Sucking water from the moist ground.

ST: *Re*→*Wi* (2 cases), *FL*→*Wi* (22), *Wi*→*Re* (4), *Wi*→*FL* (19). Most *Wi* in spring (22/24) and in females (20/24).

6. *Excreting (Ex)*: Excreting aqueous substance.

ST: Only once observed: July 30, 06:23, ♀26 (2 days old) excreted 2 drops

just before flying.

7. *Flying (FL)*: The following 5 types are distinguished by the differences in fluttering frequencies and flying speed as judged by eye. More precise measurements need to be made using appropriate equipment in future studies. In this case, no *FL* other than *roost-searching flight* were separately recorded.

1) *Wandering flight (Wf)*: Wandering from site to site on the wing. Speed ca. 1 m/s.

2) *Roost-searching flight (Rf)*: Flying about plants to search roost, characterized by a very low frequency of fluttering. Speed ca. 10 cm/s.

ST: Just or soon before *hanging (Ha)* and *sleeping (Sl)*.

3) *Female-searching flight (Ff)*: Searching for unmated females by males, made nearer the plants than *Wf*. Speed ca. 1 m/s.

ST: Short *resting (Re)* and *feeding (FE)* inserted during long *Ff* (max. 65 min).

4) *Laying flight (Lf)*: Flying about among larval host plants by females. Speed ca. 30–50 cm/s.

ST: Mostly (56.5%) after *Re* and mostly (93.3%) followed by *egg laying* including empty ovipositions (39 cases).

5) *Escaping flight (Ef)*: Speedy flight (ca. 3–5 m/s) as a result of being disturbed.

ST: Caused by interference from other animals and men during *Re*, *hanging (Ha)*, *FE* or other *flying (FL)*. A male pursued by a sparrow and another male by a dragonfly were observed. In the latter case the male ascended to ca. 5 m above the ground.

II. Interindividual behaviors

1. *Fluttering (Ft)*: Wing fluttering by non-flying males ('Flutter response' of OBARA & HIDAKA 1964; OHTANI & YAMAMOTO 1980).

ST: During *resting (Re)* (66 cases or 64.7%), *hanging (Ha)*, *feeding (FE)* and copulation.

2. *Taking-off (To)*: Start of flying by individuals in *resting (Re)* or *feeding (FE)* in response to approaching objects.

ST: Followed by mutual chasing by 2 males (*chasing gyration*) or *ascending flight* when a male in *Re* or *FE* starts out to an approaching male or a mated female. *To* in virgin females is followed by *prenuptial flight*. *To* in egg-laying females is usually followed by *escaping flight (Ef)* or *laying flight (Lf)*.

To in males was studied by OBARA and HIDAKA (1964).

3. *Wing folding (Wd)*: Mostly (108/129) by females with open wings in *resting (Re)* or *feeding (FE)* to approaching objects.

ST: During *Re*, *hanging (Ha)*, *FE* (in males and females) and copulatory conjunction (only in females). In females caused by approaching males or other butterflies mostly as a prelude to *leaning*, while in males by approaching dipterans or dragonflies, etc.

4. *Leaning (Le)*: Leaning the whole body toward approaching objects by mated and virgin females with wings usually folded. Usually preceded by *wing folding (Wd)* when wings are open, and rarely released without *Wd* ('leaning response' of OHTANI & YAMAMOTO, 1980).

ST: As in *Wd*.

SUZUKI (1979) reported *Le* as a mate avoidance behavior, OHTANI and YAMAMOTO (1980) assumed it to have an effect of 'hiding itself' in copula, based on the fact that *Le* or *Wd* of a female with *fluttering* (*Ft*) of a male was released by approaching butterflies during copulation.

5. *Abdomen erecting* (*Ae*): Keeping a posture with wings opened and abdomen erected ('mate-refusal posture' of OBARA, 1964).

Usually a mated female responds to an approaching male with *Ae*, but rarely virgin females also behave similarly (SUZUKI *et al.*, 1977; OBARA, person. comm.). In our observation 2 cases of *Ae* by virgin females were recorded: July 14, 1975 by a starved virgin female, just liberated, during *nectar intake* (*Ni*) on a flower. August 6, 1976, ♀41 just before mating.

ST: During *resting* (*Re*), *hanging* (*Ha*), *feeding* (*FE*) and *egg laying*. In 29 out of 218 cases, *Ae*→*To*→*Ef* (*To*: *taking-off*; *Ef*: *escaping flight*).

6. *Ascending flight* (*Af*) (Fig. 4, A): When a flying mated female encounters a flying male and is chased by the male, she occasionally ascends with the male up to ca. 20–30 m above the ground. Sometimes the female keeps ascending beyond the observers' sight.

Similar patterns have also been reported for *Hypolimnas misippus* (STRIDE, 1958), *Colias* spp. (SHAPIRO, 1970; RUTOWSKI, 1978), *Leptides sinapis* (WIKLUND, 1977) and *Agapetes galathea* (SONNTAG, 1981).

ST: After *chasing gyration* or *taking-off* (*To*), mostly followed by *flying* (*FL*). In 2 out of 7 cases in males, a male was chased by another male and ascended like a female (♂21 and ♂21h).

7. *Chasing gyration* (*CG*) (Fig. 4, B, C): Composed of *chasing*, *being chased* and *gyrating*.

1) *Chasing* (*Ch*): Following moving butterflies. *Ch* in males was observed much more than in females.

2) *Being chased* (*/Ch*): Flying with an individual following within a few seconds.

3) *Gyrating* (*Gy*): Mutual chasing in a circle (diam. 50–100 cm) mostly by 2 males ('a brief mutual pursuit among males' of OBARA, 1970; 'brief circling' in other species of SCOTT, 1974).

ST: During *flying* (*FL*), 96.9% in males and 53.0% in females.

8. *Swarming* (*Sw*) (Fig. 4, D): Swarming flight by more than 3 individuals, mostly performed by males. If a female, probably mated, becomes a nucleus of the swarm, both the duration of *Sw* and the number of male participants tend to increase.

OBARA (1970) also observed 'the aerial swarming flight' which occasionally contained more than 10 males and a single female.

ST: In males mostly (89.7%) during *flying* (*FL*). Only 3 cases in females: *To*→*Sw*→*Af* (♀17); *To*→*Sw*→*Ae*→*Sw*→*Af* (♀10h). (*To*: *taking-off*; *Af*: *ascending flight*; *Ae*: *abdomen erecting*)

9. *Prenuptial flight* (*Pf*) (SUZUKI *et al.*, 1977): Two types were observed.

Type-1: Zigzag to-and-fro flight by males, described by SUZUKI *et al.* (1977): "The male (under) leads the flying female (upper) to descend toward the ground by

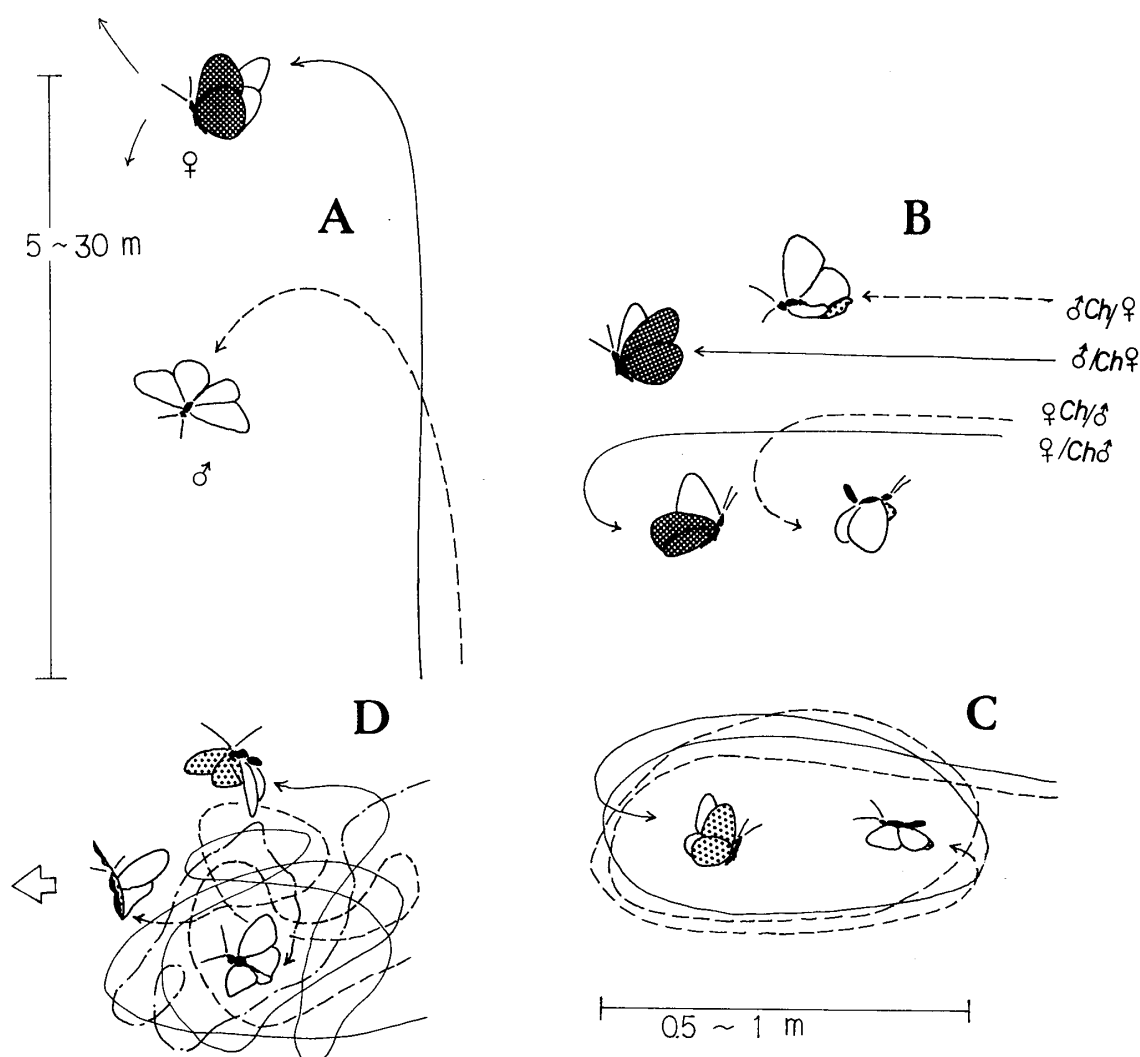


Fig. 4. Interindividual behaviors in flight. A: *Ascending flight (Af)*. A female often ascends up to ca. 30 m above the ground. A male always gives up chasing the female midway and descends earlier. B: *Chasing (Ch)* and *being chased (/Ch)* are expressed as follows: a male chasing a female ($\delta Ch/\varphi$) or a female chased by a male ($\delta/Ch\varphi$); a female chasing a male ($\varphi Ch/\delta$) or a male chased by a female ($\varphi/Ch\delta$). C: *Gyrating (Gy)* is brief mutual chasing between 2 individuals ($\delta-Gy-\delta$, $\varphi-Gy-\varphi$ or $\varphi-Gy-\delta$). D: *Swarming (Sw)*. Several individuals moving interminglingly at the speed as in *escaping flight (Ef)* (ca. 3–5 m/s). Swarming butterflies usually do not ascend over 5 m high.

this manner of flight” (from the legend of their illustration).

ST: “The female took wing soon after the male approached or touched her” (SUZUKI *et al.*, 1977). Two cases were observed: $\varphi 2$, Apr. 26, in *resting (Re)* for ca. 28 min, then she took wing and flew about together with a male for 35 s, and then alighted on a grass and copulated with the male; $\varphi 5$, July 1, *Ni* (35 s) \rightarrow *To* \rightarrow *Pf* (30) \rightarrow copulation. (*Ni*: nectar intake; *To*: taking-off)

Type-2: Zigzag flight by females. In 7 cases a virgin female flew to an approaching male (i.e. *To*), and went ahead of a male in a zigzag manner at a good speed (near one of *escaping flight (Ef)*).

A male followed a female at a distance of several cm and eventually succeeded in copulating with her. In 4 cases each male did not continue to chase the virgin female (♀4; ♀10) flying in the manner of type-2 and missed her.

ST: Succeeded 4 cases: ♀10h, May 9, *Re* (2785 s) → *To* → *Pf* (20) → copulation; ♀3, June 25, *Re* → *To* → *Pf* (120) → copulation; ♀10, July 7, *FL* (35) → *Pf* (25) (with ♂11) → *FL* (15) → *Gy* (with a female) → *FL* (5) → *Pf* (15) (with an unmarked male) → copulation. (*FL*: flying; *Gy*: gyrating)

SUZUKI *et al.* (1977) did not distinguish type-2 from type-1, probably because their observations were made in a field cage where the males can easily find the females regardless of the females' sexual urge. We often observed that flying males were unable to find females resting in the Campus field.

III. Temporally integrated behaviors

1. *Mating (Mt)*: Interindividual actions between a male and a female, mainly led by the male. Seven component patterns except *pair-bond flight* are probably linked together by a mating drive.

1) *Prenuptial flight (Pf)*: Aforementioned. *Pf* in 2 cases were omitted when the resting female did not take wing.

2) *Keeping closed (kc)*: By females, alighting on some substrata after *Pf* and keeping motionless with wings closed until *nuptial flight*. "About 7 seconds from the male's approach to the beginning of nuptial flight" (SUZUKI *et al.*, 1977).

3) *Paralleling (pa)*: By males, alighting soon after *kc* by the female, and sitting side by side with her.

4) *Catching wings (cw)*: By males. "The male continuously fluttered his wings and caught the female by the costae of the fore wings with his fore legs and a mid leg" (SUZUKI *et al.*, 1977).

5) *Grasping genitalia (gg)*: By males. The male "curved his abdomen dorso-laterally, inserting it between the hind wings of the female to take hold the tip of her abdomen with his genitalia. At the same time he opened his wings to 120–170°, especially depressing one side that faced her" (SUZUKI *et al.*, 1977).

6) *Nuptial flight (nf)*: "The pair had usually no sooner copulated than the male took a short flight, the male carrying the female upside-down with her wings closed" (SUZUKI *et al.*, 1977).

7) *Copulation (co)*: Conjunction of genitalia of both sexes, lasting about 1 h (8 cases, 4203.8 ± 1515.9 , SD).

8) *Pair-bond flight (bf)*: Flying by a male in copula with a female when the pair was approached by big animals (dogs, men etc.) or persistent males during *co*. Same pattern to *nf*, but variable duration.

ST: Transitions from *prenuptial flight (Pf)* to *keeping closed (kc)* (i.e. unsuccessful mating) were observed in 6 out of 9 cases. During *copulation (co)*, to the approaching object, the female responds with *wing folding (Wd)* or *leaning (Le)*, while the male with *fluttering (Ft)* or *taking-off (To)*. *To* by the male results in *bf*. After *co*, the male releases genital contact. The female, previously hanging upside-down from the male, is obliged to walk downward soon after being released. Thereafter,

they fly away independently.

2. *Egg laying (El)*: A sequential pattern composed of 4 component patterns.

1) *Laying flight (Lf)*: Aforementioned. Rarely omitted at successive egg laying.

2) *Drumming (dr)*: Alighting on plants for oviposition, and tapping fore legs alternately up and down ('drumming reaction' in *Pieris brassicae*, ILSE 1937); 'drumming' in 7 butterflies, ILSE 1955; 'tarsal scratching' in *Leptidea sinapis*, WIKLUND 1977).

According to ILSE (1955), the sound was often audible, but I could not hear it.

The function of *dr* is uncertain (LUNDGREN, 1975). 'A wind making behavior' was suggested by TEROFAL (1965) who explained that *dr* whirled up the scent saturated air from the leaf surface, but also showed that females with amputated fore legs could find their foodplants.

3) *Pressing abdominal tip (pr)*: Bending the abdomen and pressing its tip on the under surface of the leaf by the female usually in the hanging posture.

4) *Oviposition (ov)*: Adherence of an egg on the oviposition site (usually foodplants). Short *laying flight (Lf)* is often inserted during successive egg laying.

ST: Followed by *resting (Re)* (62.3%), *flying (FL)* (14.5%), *nectar intake (Ni)* (10.8%), *chasing gyration (CG)* (7.6%), *Lf* (3.6%) etc.

In this open catalog, I split a behavior pattern whenever I could distinguish differences in it (e.g. type-1 and type-2 in *prenuptial flight (Pf)*). It is better for the survival of data to be a 'splitter' rather than a 'lumper' in classification at the beginning of a study. ALTMANN (1965) said that the rule of thumb was to split when in doubt and later the categories could be lumped if the differences between the categories did not appear to be significant. Only in the case of *Re*, might I have been a 'lumper'.

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摘 要

野外で観察されたモンシロチョウ成虫の行動 I. 行動目録 (大谷 剛)

1976年4月末から8月末にかけて北海道大学の構内でモンシロチョウの個体追跡を行い、観察された行動の目録をつくった。市販のマジックインク(赤)でマークされたオス11個体メス20個体の行動追跡データに基づいて、35種類に分類した行動型は次のとおり:

<単独行動>

不活動(IN): 休息(Re) —1*, 下垂休息(Ha) —2*, 睡眠(Sl) —3*.

体掃除(Sc): 4*.

頭振り(Hr): 5*.

歩行(Wa): 6*.

採餌(FE): 吸蜜(Ni) —7*, 吸水(Wi) —8*.

排出 (Ex): 9.

飛翔 (FL)*: 移動飛翔 (Wf) —10, ねぐら探し飛翔 (Rf) —11, 探雌飛翔 (Ff) —12, 産卵飛翔 (Lf) —13, 逃避飛翔 (Ef) —14.

＜個体間行動＞

はばたき反応 (Ft): 15*. 飛びたち反応 (To): 16*. 翅閉じ反応 (Wf): 17*. 傾き反応 (Le): 18*. 尻あげ反応 (Ae): 19*. 上昇飛翔 (Af): 20. 追尾回転飛翔 (CG). 追尾 (Ch/): 21. 被追尾 (Ch): 22. 回転 (Gy): 23. 群飛 (Sw): 24. 前交尾飛翔 (Pf): 25.

＜行動環行動＞

配偶行動 (Mt): 静止 (kc)♀ —26, 横並び (pa)♂ —27, 翅つかみ (cw)♂ —28, 尻曲げ (gg)♂ —29, 交尾飛翔 (nf) —30, 交尾 (co) —31, 結合飛翔 (bf) —32.

産卵行動 (El)♀: ドラミング (dr) —33*, 腹部押しつけ (pr) —34*, 産卵 (ov) —35*.

以上の中で, 4 は頭部掃除だけが観察された. 5 は, 飛翔前に時々みられる頭部を左右に振る行動. 4 によく似ているが, 前肢の動きはない. 9 は 1 回のみ観察され, 早朝の飛び出しの直前に液状のものを排出した. また, 25 については, オスが積極的なタイプ 1 とメスが積極的なタイプ 2 を区別した.

星印をつけた行動型については, 動きうる体各部 (Fig. 1) の組み合わせによる記載を試みた (Table 1). しかし, 配偶行動や個体間行動の多くのものは表ではうまく記述できないので, 簡略化した文章による記載に, その行動型が生じる前後の状況 (ST: で始まる部分) の記述を添え, 本文とした.

省略記号は, 2 文字のアルファベットでつくり, 独立した行動型は大文字と小文字, 便宜的にいくつかの行動型をまとめたものは大文字のみ, 単独では現れず 1 つの「行動環」としてのみ現れる行動型は小文字のみで構成した.

行動型はできるだけ細かく区別したが, 休息 (Re) 中にみられる「日光浴行動」と「日光避け行動」は必ずしも典型例ばかりでないで, 区別しなかった.